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A Guide to the Snake Hemipenis: a Survey of Basic Structure and Systematic Characteristics

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(Plates I-III; Text-figures 1-6)

THE structures of the male genitalia of snakes were first used as systematic characteristics by Edward Drinker Cope (1893, 1894, 1895, 1900) in a brilliant attempt to introduce new dimensions into the classification of the suborder Serpentes. Cope's studies were based upon an analysis of the hemipenis in more than 200 species of snakes that are representative of all currently recognized familial groups except the Typhlopidae, Leptotyphlopidae, Xenopeltidae and Uropeltidae. His material indicated clearly that not only are the hemipenial structures of value to the student of major classification but in addition they may also be employed to distinguish between genera, and on occasion between related species.

Unfortunately, few herpetologists have taken advantage of the foundation provided by Cope and the nature of the hemipenes of most snakes remains to be studied. A number of factors seem to have contributed to this reluctance to use penial features in systematic studies. Among the more pertinent objections are: (1) rejection of the use of internal characteristics in systematic work (Constable, 1949, p. 59); (2) dislike of utilizing features found in only one sex as a basis for classification (McCann, 1946); (3) a belief that the hemipenes are difficult to locate and prepare for study; (4) lack of understanding regarding the basic structure and characteristics of the hemipenes, intensified by the inconsistent terminology applied by Cope and the misapplication of certain of his terms by subsequent workers; (5) confusion, due primarily to (4) above, as to the nature of hemipenial variation and consequent distrust of decisions formulated from penial evidence. In our opinion, none of the listed criticisms of the application of hemipenial characters in snake taxonomy is valid. Certainly, the philosophy which objects to the use of internal features in classification cannot be taken seriously by modern systematists. Neither can we accept the suggestion that hemipenial features are not significant merely because they are found only in males. Ample precedent exists for systematic evaluation based upon organs (frequently sexual) restricted to only one sex in such diverse groups as birds, fishes, insects, cephalopods and higher plants. Of course we do not advocate a classification based solely on the characters of the male genitalia, but rather one in which genital structures are used in combination with other features.

The remaining three objections to utilization of hemipenial characters in classification are empirical rather than philosophical. They appear to constitute the chief reasons for the indifference of most herpetologists to the use of penial features in taxonomy. Since the hemipenis, as will be shown below, is relatively easy to ready for study, the belief that it is difficult to locate or prepare is fallacious. Criticism of the use of the hemipenes because of confusion regarding their morphology combined with an inconsistent and inadequately defined descriptive terminology is well taken. Different authors have used the same terms for totally different structures or have coined different terms for the same structures. The result has been a chaotic pattern of non-comparable descriptions and has effectively reduced the reliance of systematists upon hemipenial data. However, it has been the application of terms—not the condition of the organs—which has caused the difficulty. In papers with an internally consistent approach

(Pope, 1935; Bogert, 1940; Smith, 1943) the validity of hemipenial characters as systematic tools has been fully demonstrated. The obvious remedy for this somewhat confused situation is development of a standardized terminology for description of the hemipenis, not in the rejection of penial features as taxonomic characters. Finally, the lack of knowledge concerning penial variation is more apparent than real and stems directly from the confusion surrounding morphologic description. Although we have not undertaken an extensive analysis of variation in hemipenial characters as part of the present report, we are convinced on the basis of information in the literature and our own studies that the limits of penial variation are no greater than for other morphological features and that if properly described the hemipenial characters form a firm foundation for systematic decisions.

The primary aims of the present paper are to take advantage of the previous work on hemipenial structure and to overcome the problems mentioned in the preceding paragraph by describing methods of preparing the hemipenis for analysis and in establishing a standardized terminology for the description of penial characters. It is our belief that the standardized treatment here proposed, if accepted by other herpetologists, will result in further clarification of the significance of penial variation and will form a sound basis for expanding the use of hemipenial characters in serpent systematics.

Acknowledgments

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Most of the hemipenes described herein are currently held in the private collection of the senior author (HGD), pending further study. The original drawings are the work of Mrs. Frances Waite Gibson, University of Arkansas, Fayetteville. This study was made possible by the financial support of the National Science Foundation (NSF G-4443; NSF G-9719).

Use of Hemipenial Characters in Snake Systematics

Cope (1893, 1894) in a bold attempt to break away from the classification of snakes developed by Boulenger (1893) from the system devised by Constant Duméril (see Duméril, Bibron & Duméril, 1854), first employed the structural characteristics of the hemipenis in systematics. The classification set up by Duméril emphasized scutellation, cranial osteology and dentition. Boulenger had modified the system primarily through utilizing Cope's (1886) work on vertebral hypapophyses. Cope, however, undertook to discern features of phyletic significance in the soft anatomy of snakes, notably in the lungs and male genitalia, as an aid toward the development of a more natural classificatory system. Subsequent to his preliminary reports of 1893 and 1894, Cope published a comprehensive work (1895) detailing the characters of the lungs and hemipenes for a great number of ophidian species. His revised classification was based upon a combination of characters including those of the genital and pleural features. The paper includes 20 plates illustrating approximately 235 hemipenes and, while the descriptions and figures are on occasion inadequate or erroneous, the report stands as a major contribution to the understanding of serpent classification. (These plates were later published in a reduced size, Cope, 1900). Although originally interested in the penes as aids in setting up a major classification of snakes, Cope also demonstrated that the hemipenial characters were of general value in distinguishing between related species and genera.

Since Cope's day, the hemipenial characters have been employed both for segregation and integration. However, the majority of workers have restricted themselves to either one or the other of these taxonomic functions, with emphasis on the discriminatory phase. The principal attempt to utilize penial features for major classification, since 1900, has been by Dunn (1928), who arranged the genera of American colubrids on the basis of a combination of vertebral, dentitional and hemipenial characters. Bogert (1940) applied a similar procedure in evaluating the African colubrids, but rejected Dunn's major divisions founded upon penial features as being polyphyletic. His conclusions indicated that both Cope and Dunn may have been too sanguine in their estimate of the importance of hemipenial features in major classification. Bogert also demonstrated that, within limits, certain penial characteristics are restricted to groups of related genera and thus he does not entirely rule out the hemipenes as having significance in supra-

generic classification. Vellard (1928a, 1928b, 1946) is the only other student to deal with hemipenial features as they relate to problems of major classification. A number of significant analyses of differences between species and genera have appeared, especially Domergue (1955), McCann (1946), Pope (1935) and Smith (1943). In addition an impressive array of North American herpetologists have described hemipenes in their specific and generic revisions.

Data from these several sources together with our own work on snake penes make possible certain conclusions regarding the current status of hemipenial characters in relation to modern systematic studies:

(1) It has been amply demonstrated that the features of the hemipenes are rather stable for a particular species or species group and when properly analyzed may provide a means of systematic discrimination between related taxa.

(2) The range of interspecific and intraspecific variation in hemipenial characters needs further investigation in order to establish confidence limits on the patterns of variation exhibited within a species population.

(3) The characteristics of the hemipenis are also useful in evaluating the degree of relationship between forms and in combination with other features may provide a basis for infrageneric, generic and suprageneric groupings of species.

(4) The phyletic significance of differences in the hemipenes at the suprageneric levels is not now known and penial structures cannot at present be used in delimiting higher categories of snakes. Vellard's (1946) interesting attempt to construct a phylogeny of snakes based on hemipenial characters is derived from study of too few genera to make it convincing.

In general we believe that the structural features of the hemipenes ought to be utilized in snake systematics to a much greater extent than in the past. The organs provide a number of additional characters for evaluation over those of osteology, lepidosis, coloration and measurements. Only through a continued and increased analysis and application of data on penial features to the solving of problems in serpent systematics can the full value of these characters be realized. It is hoped that the present paper will serve to some degree as a stimulus to more accurate and more frequent utilization of the characters of these organs in classification.

Basic Structure of the Hemipenes

The structure of the squamate hemipenis has been described by a number of morphologists, but the papers by Beuchelt (1936), Unterhossel (1902) and Volsøe (1944) are the most useful and comprehensive. The publications of these authors have been extensively utilized in preparing the section on the anatomy of the organs. However, questionable points have been verified by dissection.

The hemipenes of snakes are paired tubular membranous organs lying in the base of the tail ventral to the horizontal septum and separated from the lateral and subcaudal integument by thin layers of superficial ventral body muscle, the paired medial *m. rectus caudae,* and connective tissue. The hemipenes are hollow and each organ opens to the exterior through an aperture on the lateral margin of the posterior lip of the cloacal opening. The hemipenes are ventral to the glandular anal sacs, which in females may be greatly enlarged and occupy much of the space filled by the genitalia in males. The anal sacs of males empty into the cloaca through small pores at the posterior margin of the cloacal slit lateral to the openings of the hemipenes. Each anal sac is covered by a well-developed muscle (*m. constrictor sacculi ani*) which serves to expel a glandular secretion into the cloacal region.

Each hemipenis is a cylindrical organ composed of two primary membranous and erectile layers. When the hemipenis is retracted or in an invaginated state, the most superficial portion is the undifferentiated asulcate layer. The internal sheath, or sulcate layer, (Pl. I, Fig. 1) is undifferentiated on its outer surface. However, the inner surface, which borders the central lumen of the organ, is traversed by a deep, well-defined groove, the *sulcus spermaticus,* and is frequently ornamented with a series of complex structures. The entire sulcate layer is permeated by a series of lymph sinuses. Lying between the asulcate and sulcate layers is a large sinus that becomes filled with blood at the time of penial erection. This sinus may be divided somewhat by a series of thin projections of connective tissue which extend for short distances along the longitudinal axis of the organ from the asulcate to sulcate layer. These projections probably function to support and attach the two layers while the organ is evaginated. Essentially, the hemipenis is made up of two hollow cylinders of tissue, one (sulcate) inside the other (asulcate), that are narrowly separated by a hollow blood sinus.

In describing the retracted organ, (Pl. II, Fig. 3) the following series of definitions are recommended for reference to direction, orientation and relative position of parts. The portion of the organ located near the cloaca is proximal or basal. That portion lying most posterior in the

tail is distal or apical. The terms dorsal and ventral refer to the areas of the organ located nearest to the vertebral column and subcaudal surface of the tail, respectively. The structures of the hemipenes situated nearest to the sides of the tail are lateral, while those found adjacent to the longitudinal plane of the tail are medial.

Associated with the hemipenes are a series of specialized muscles. Dorsal and lateral to the organs are paired propulsor muscles that extend from the base of the tail for a considerable distance posterior to the hemipenes. The propulsor muscle sheath originates from a band of fascia attached to the caudal chevrons, which in snakes are fused to the ventral surface of the caudal vertebrae, and extends ventrally around the anal sac, the hemipenis and other penial muscles to insert on the median septum of the tail. Three retractor muscles, which lie within the area inclosed by the propulsors, insert on each hemipenis. The *m. retractor penis magnus* originates on one of the posterior caudal vertebrae and extends anteriorly to insert on the distal end of the hemipenis. This muscle may be divided for some distance posterior to its points of attachment to the hemipenis in species with a divided or bilobed organ and one slip is inserted on each of the penial apices. The *m. retractor penis parvus* originates on one or more of the anterior caudal vertebrae medial to the propulsors and inserts by a tendon on the dorsal asulcate surface of the penis. The *m. retractor penis basalis* originates from the ventral abdominal wall below the urogenital papilla and inserts via a fascia on the asulcate surface of the hemipenis.

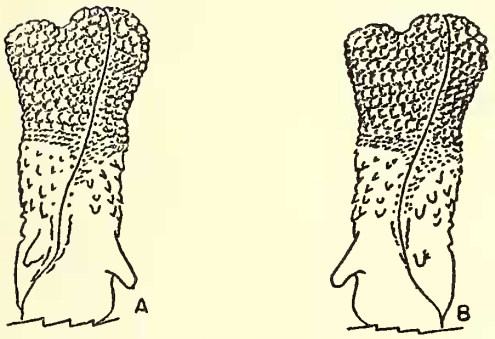
At the time the organ is everted or evaginated the lymph sinuses of the sulcate layer and the blood sinus between the asulcate and sulcate layers become filled with fluids, the former from the *cysterna lymphatica* of the cloacal region and the latter by a penial vein (Pl. I, Fig. 2). The lymph and blood first fill the sinus cavities in the basal portion of the hemipenis. At the same time the retractor muscles are relaxed and the propulsor muscles contract to evert the basal portion of the organ. Apparently only the basal segment is normally everted by most species prior to actual insertion of the hemipenis into the female cloaca. Only one of the organs is utilized in copulation at any one time (Boulenger, 1913, p. 83, and McCann, 1946, are in error) although both may be partially everted. The recent erroneous reference to the simultaneous insertion of both hemipenes in ***Pseudaspis cana*** (Brain, 1959) is based upon observations of a species with a divided hemipenis of exceptional length (*vide* Bogert, 1940, p. 42).

Once the hemipenis has been inserted into the female an increase in blood and lymph pressure evaginates the remainder of the organ. This process produces an organ fully extended with fluid in which the sulcate layer now lies on the exterior surface and the asulcate layer is internal to it (Pl. II, Fig. 4). Thus the hemipenis has been turned completely inside-out so that the sulcus spermaticus is on the external surface and is now in position to transport spermatozoa from the male cloaca into that of the female. It is assumed that in species with a bifurcate sulcus, each branch terminates near to the corresponding oviductal openings in the female cloaca (Pope, 1941). Snakes with hemipenes in which the organ is divided at the tip insert each of the separate apices into depressions of the cloaca dorsal to the openings of the oviducts. The ornamentation on the sulcate surface, which is now the external surface, becomes fully extended and serves to anchor the penis rigidly within the cloaca. In most species the organ cannot be removed from the female without damage to both copulating individuals unless the male undertakes penial retraction.

Although the everted hemipenis is basically similar to a retracted organ turned inside-out, the fully protruded penis is no longer strictly cylindrical, nor do its various structures retain precisely the same positions they held when in the invaginated condition. Usually there are marked differences apparent in the diameter of the basal and apical areas and differentials in the elasticity of the investing tissue of the sulcate layer produce asymmetry and some twisting of the organ. The sulcus spermaticus, for example, frequently runs partially around the hemipenis in its course from cloaca to tip, while in the retracted organ the sulcus forms essentially a straight line. Because of the distortions produced by eversion, comparable parts no longer retain the identical relationship to the major axes of the snake. In consequence the points of reference used for orientation and direction on the protruded organ must be defined somewhat differently.

In a snake with a fully extruded hemipenis the organ may project anteriorly, posteriorly or laterally from the cloacal region. However, if the hemipenis is gently depressed into a position where the apex points directly downward (at 90° to the anal slit), a logical and adequate system of directions may be established (Pl. II, Fig. 4). The portions of the organ lying nearest to the cloaca are basal and retain the same relationship to the remainder of the hemipenis as do the basal areas of the retracted organ. The free tip is referred to as the apical end and corresponds to the same region in unprotruded

hcmipenes. The side of the organ having the major length of the sulcus is designated the medial surfacc, while the opposite side is lateral. The basis of this definition may be seen in thc organs illustrated. The sulcus enters the hemipenis on its anterior surface (toward the cloaca) and on a right hemipenis (Text-fig. 1B) turns sharply left (medially), while on a left hemipenis (Text-fig. 1A) the sulcus turns sharply right (mcdially).



TEXT-FIG. 1. Left (**A.**) and right (**B.**) hemipenes of *Masticophis flagellum* (HGD 38), showing their asymmetrical structure. Note that the organs are mirror-images near their bases but are more nearly identical toward their distal ends.

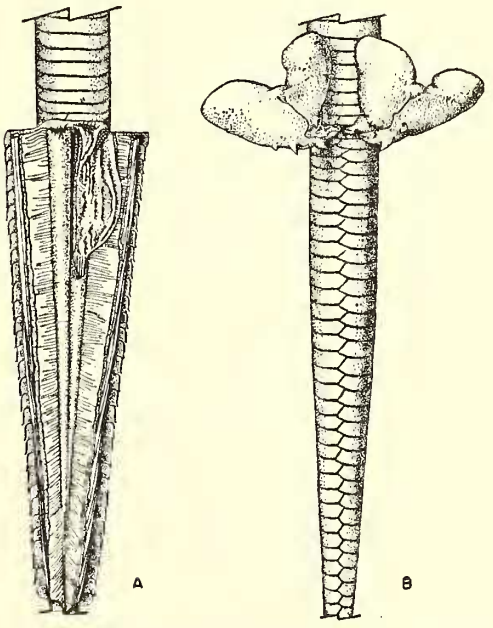
The invagination of the hemipenis apparently is accomplished by reduction in lymphatic and blood pressure in conjunction with contraction of thc retractor muscles. Initial retraction is produced by the action of the *m. retractor penis magnus,* which inverts the apical portion of the hemipenis. After the apical region is invaginated the *m. retractor penis parvus* retracts the more basal areas until only the base still protrudes. The final stage in retraction is accomplished by deturgescencc of the base and contraction of the *m. retractor penis basalis.* The propulsor muscles remain relaxed during thc retraction process.

Descriptive Features of the Hemipenes

The completc description of a hemipenis for systematic purposes includes information on its length, shape, condition of sulcus spermaticus, nature and pattern of ornamentation and type of apex. Inasmuch as the right and left hemipenes of the same individual usually differ somewhat from one another and vary in different species from almost exact mirror images to almost identical organs (Text-fig. 1), it is essential to indicate which of the two hemipenes is described. As a standard procedure we recommend that descriptions of *in situ* organs be based upon thc lcft hemipenis, while the right organ is to bc uscd for dcscription of the everted hemipenis. Since everted hemipenes can be prepared only from freshly killed speicmens, the right organ must be routinely and fully protrudcd before thc snake is preserved.

Preparation

In Situ.—Much of the necessary information may bc gained from examination of museum specimens in which the hemipenes have been preserved in a retracted position. In fact Cope (1895), Pope (1935), Bogert (1940) and Smith (1943), use this method as their standard. For proper observation, the ventral surface of the tail is slit down or just off the mid-line from two caudals behind the cloaca posteriorly for a distance of 20 or more caudals. The hemipenes will be seen as soon as the integument and thin muscle are separated away from them by spreading the incision. Additional separation of tissuc will free the hemipenis from the surrounding area. Once the organ is exposed it is cut along its medial longitudinal surface and spread out flat for study. Although a medial slit usually avoids damage to the sulcus spermaticus, thc latter structure may on occasion be bisected. For purposes of orientation the incision marks the longitudinal axis of the medial surface of thc *in situ* hemipenis. Thc organ may be left in position for general obscrvation (Text-fig. 2A), al-



TEXT-FIG. 2. Appearance of hemipenes: **A.** Viewed as inverted organs after slitting the ventral wall of the tail. **B.** Viewed as everted organs.

though the *m. retractor penis magnus* usually must be cut some distance posterior to the hemipenis. If the penis is to be described in detail or used for illustration it should be removed from the snake and pinned out flat on a board.

Everted.—It must be recognized that the information taken from a dissected specimen is not complete. The approximate length, the condition of the sulcus and the general features of ornamentation are observable *in situ*. However, the relationships of the various parts of the irregularly cylindrical organ are difficult to determine in the retracted state and it is practically impossible to gain any idea as to the shape of the hemipenis. For these reasons everted preparations are much to be preferred. As mentioned above, the right hemipenis should be everted in freshly killed specimens. Frequently, partial extrusion may be accomplished by manual pressure applied at the base of the ventral surface of the tail, a short distance posterior to the anal opening. Usually it is more effective to slit open the ventral surface of the tail, cut the *m. retractor penis magnus* and inject fluid into the blood sinus at the base of the hemipenis so as to cause eversion. It is sometimes useful to cut the everted organ at its base, after it has been fixed in preservative, and to tie the base off with a thread. This latter procedure is not recommended until the length and orientation of the organ have been noted. The technique is most helpful if the particular hemipenis is to be illustrated. Ortenburger (1923) discusses the use of bees-wax and paraffin in making everted preparations. Liquid latex may also be used for injection into the blood sinus. The preparator is warned that the organ must be fully extended before fixation if it is to be of any systematic value, otherwise the important terminal structures will be hidden. The difference between an everted organ and one seen dissected *in situ* is striking (Text-fig. 2B).

Hemipenial Characters

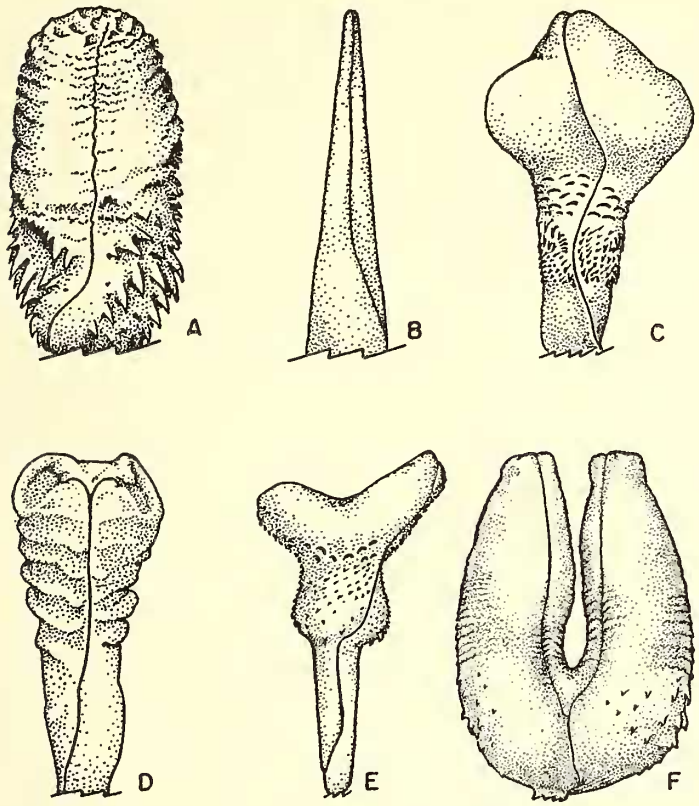
The following account presents an outline of systematic characters and a standardized terminology for description of the snake hemipenis. Whenever possible reference is made to the occurrence of the different structural features in the several families of serpents. For the sake of convenience we employ the classification proposed by Dowling (1959a), which recognizes nine families: the Typhlopidae, Leptotyphlopidae, Boidae, Anilidae, Xenopeltidae, Uropeltidae, Colubridae, Elapidae (includes the Hydrophiidae) and Viperidae (includes the Crotalidae). The hemipenes of the Typhlopidae and Leptotyphlopidae are unknown, except for the descriptions by Smith (1943, p. 43) for the former, and by Bailey & Carvalho (1946, p. 5) for the latter.

Points of Reference.—The structures of the hemipenis may be recorded with reference to the caudal level. In practice there appears to be little difference between *in situ* and everted organs with regard to basic organization and the general relation and position of significant parts. The length of the organ, the point at which the sulcus bifurcates or the hemipenis divides and the exact extent of the various areas of ornamentation provide a number of useful systematic characters. As an example in the colubrid *Atractus elaps,* the base of the organ is covered with small spines to the level of the fourth or fifth caudal and with large spines from that point to the level of sulcus division; flounces replace the spines at the sulcus division and extend to the apex of the organ; the sulcus spermaticus bifurcates at the level of the eighth or ninth caudal; the tip of the organ reaches to the level of caudal 12 or 13.

Length.—The length of the hemipenis is frequently of significance in systematic discrimination and is recorded as previously indicated with reference to a particular caudal level. While there is obviously some variation to be expected in such a membranous organ, depending upon the degree to which the retractor muscles are contracted, the variational range appears to be less than 20 per cent. of the total length of the organ. In most forms, the hemipenis rarely varies more than two or three caudals in total length. For example in the green ratsnake, *Elaphe triaspis intermedia,* the hemipenis is found to extend posteriorly to caudal 25, 26, 27 or 28. The range of variation is greatest in long hemipenes. Intergeneric variation is much greater. In the African colubrid genera studied by Bogert (1940), as an example, the hemipenis was found to be as short as only three caudals in *Psammophis,* while it terminated at the level of the 32nd caudal in *Pseudaspis.* The organ in other African genera reached the following wide variety of caudal levels: 4, 5, 6, 7, 8, 9, 10, 13, 14, 15, 16, 17, 18, 19, 20, 23, 24.

In addition to recording the length of the organ it may also be useful to indicate the caudal level at which the *m. retractor penis magnus* divides in snakes with a double hemipenis and to determine upon which vertebrae the *m. retractor penis magnus* and *m. retractor penis parvus* originate.

Shape.—Less information is presently available on hemipenial shape than on any other feature. Although certain aspects of the general form of the hemipenis can be determined from



TEXT-FIG. 3. Hemipenial shapes: **A.** Single subcylindrical organ (*Spalerosophis diadema,* HGD 16). **B.** Single attenuate organ (*Psammophis sibilans,* redrawn from Bogert, 1940, fig. 14). **C.** Single bulbous organ (*Spilotes pullatus,* HGD 199). **D.** Single clavate organ (*Charina bottae,* HGD 178). **E.** Bilobed organ (*Elaphe obsoleta,* HGD 202). **F.** Divided organ (*Crotalus viridis,* HGD 187).

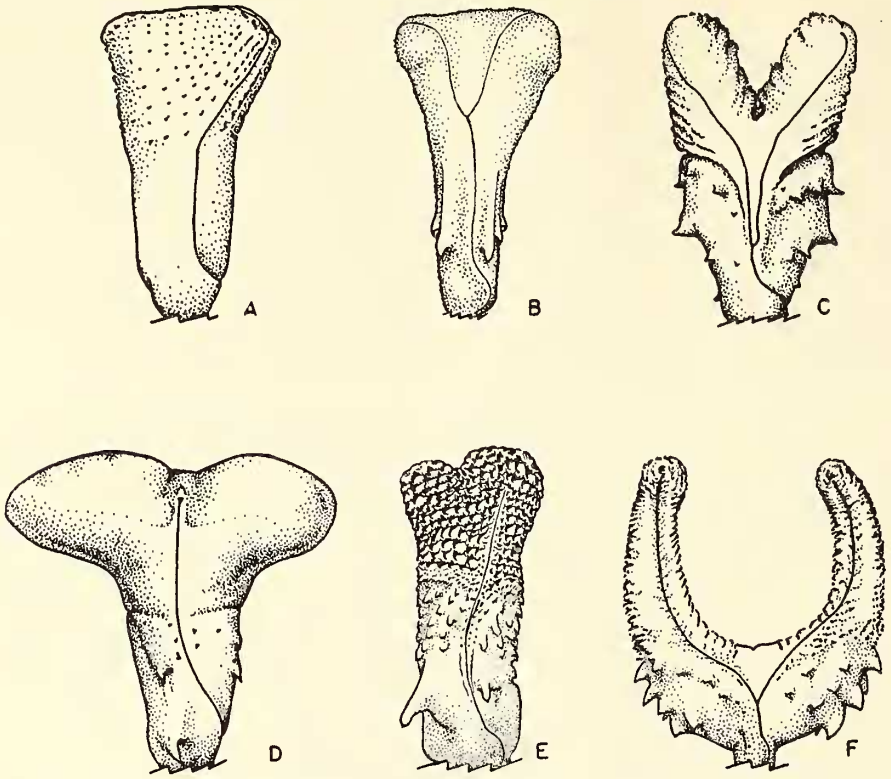
in situ preparations, the organ must be everted for evaluation of the characteristics of shape. The hemipenis may be *single, bilobed* or *divided* in basic form. The single types are found in some boids, some anilids, uropeltids, many colubrids and elapids. The single hemipenis is essentially a modified cylinder, although its tip may be asymmetric and irregular, and there is no evidence of a division of the apex into two parts. Some single organs are *subcylindrical* (Text-fig. 3A), others are sharply tapering or *attenuate* (Text-fig. 3B), *bulbous* (Text-fig. 3C), or *clavate* (Text-fig. 3D).

Bilobed organs are those in which the hemipenis is divided only at the apex, for a distance less than the length of the undivided basal segment (Text-fig. 3E). Bilobed hemipenes have been described in the Boidae, Anilidae, Xenopeltidae, Colubridae, Elapidae and Viperidae. *Divided* organs may be defined as hemipenes in which the basal undivided portion is equal to, or shorter than, the apical segments (Text-fig. 3F). Divided hemipenes are known from all snake families having bilobed types, except for the Anilidae and Xenopeltidae, and there is a gradual gradation from divided into bilobed types. Bilobed and divided organs may also be subcylindrical, attenuate, bulbous or clavate in form. In some species the organ is coiled or *cirrate* (Brain, 1959) and although this condition is currently known only in forms with double hemipenes, it seems likely that snakes with single cirrate organs ultimately will be discovered.

Stull (1928) has figured and described several species of the boid genus *Tropidophis* in which the two lobes of an essentially divided hemipenis are themselves divided to form a quadruple organ with four apices. However, Schwartz & Marsh (1960) recently have shown Stull to be in error and no snakes are known to have this condition.

Sulcus Spermaticus.—The sulcus spermaticus is a longitudinal groove on the outer surface of the everted hemipenis which serves to transport the spermatozoa from the male into the female cloaca. The margins of the sulcus are usually clearly marked by fleshy lips in *in situ* preparations. These lips lie on each side of the groove and frequently contrast markedly with adjacent areas of the hemipenis, although in some cases they exhibit a degree of ornamentation. When the organ is everted and becomes completely swollen with fluid, the lips come to form the walls of the sulcus and often are not visible on the surface of the organ (Text-fig. 4).

The sulcus spermaticus may be either *simple*

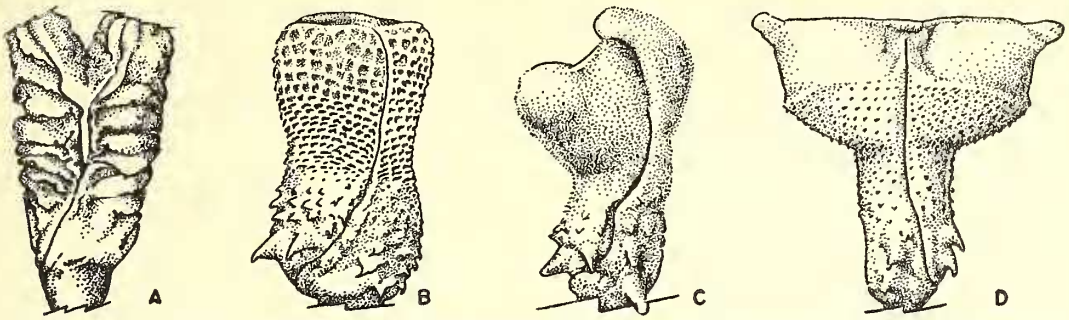


TEXT-FIG. 4. Sulcus spermaticus structure: **A.** Simple oblique sulcus on single organ (*Lampropeltis calligaster,* HGD 514). **B.** Bifurcate sulcus on single organ (*Denisonia superba,* HGD 182). **C.** Bifurcate sulcus on bilobed organ (*Heterodon platyrhinos,* HGD 512). **D.** Simple straight sulcus on bilobed organ (*Natrix erythrogaster,* HGD 517). **E.** Simple oblique sulcus on bilobed organ (*Masticophis flagellum,* HGD 38). **F.** Bifurcate sulcus on divided organ (*Agkistrodon contortrix,* HGD 516).

or *bifurcate* in single (Text-figs. 4A-B) or in bilobed hemipenes. When bifurcate on a bilobed organ, one branch of the sulcus extends up each lobe (Text-fig. 4C), but when the sulcus is simple on such an organ it may extend to directly between the lobes (Text-fig. 4D) or up one of the lobes to near its apex (Text-fig. 4E). The sulcus is bifurcate in species with a divided hemipenis (Text-fig. 4F).

Hemipenes with a simple sulcus are definitely known in only three families, the Anilidae, Uropeltidae and Colubridae, although Cope (1895, pl. 15, fig. 3) indicates the occurrence of a simple sulcus in one boa (*Epicrates striatus*). Cope's observations and plate probably are in error since no other boid is known to have a single sulcus and other members of the genus *Epicrates* examined by us (see also Vellard, 1946) have a bifurcate sulcus (Text-fig. 5A). All snake families so far investigated, except the Uropeltidae, have representatives with a bifurcate sulcus. All members of the families Xenopeltidae, Elapidae and Viperidae, so far studied, have organs with a bifurcate sulcus. The Boidae, with the questionable exception noted above, also belong here.

Ornamentation.—The majority of snakes have hemipenes that are covered for most of their length by specialized structural modifications. Usually the extreme basal area is *naked* and in some forms the entire organ lacks ornamentation (Text-fig. 3B). Naked organs of this general type are known in the African colubrid genera *Malpolon* (Domergue, 1955, pl. 24, fig. 4), *Psammophis* (Bogert, 1940, p. 80) and its allies *Cerastes, Dromophis, Hemirhagerrhis, Mimophis* and *Rhamphiophis,* and in *Prosymna* (Schmidt, 1923, p. 89). Cope, 1895 (pl. 15, fig. 9) indicated that *Calamaria* has a naked organ, but Pope (1935, p. 307) demonstrated that Cope was in error. Most species of snakes have hemipenes that are *ornamented* except basally. Organs that have the major portion of the sulcate surface covered by a homogeneous and uniform ornamentation are *undifferentiated.* Those in which there are different kinds of orna-



TEXT-FIG. 5. Gross ornamentation: **A.** Flounced (*Epicrates angulifer*, HGD 180, not fully everted). **B.** Calyculate (*Opheodrys aestivus*, HGD 20). **C.** Papillate (*Leptophis mexicanus*, HGD 66). **D.** Spinose (*Thamnophis radix*, HGD 173).

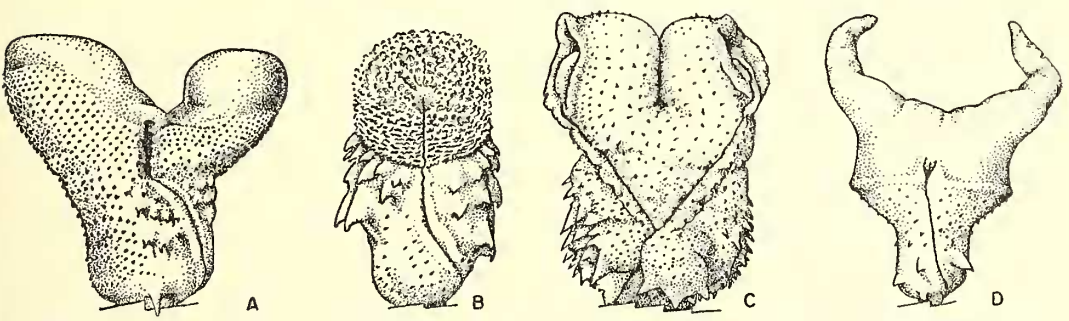
mentation at different levels along the hemipenis are *differentiated.*

The principal types of ornamentation are *flounces, calyces, papillae* and *spines*. Flounces are simple linear ridges or folds of tissue which parallel one another and encircle the hemipenis (Text-fig. 5A). Most boids, *Xenopeltis* and some anilids, colubrids, elapids and viperids, have flounced hemipenes. As suggested by Cope (1895, pl. 14, figs. 2, 3, 5) flounces may be either transverse or oblique (pinnate). Typical colubrids and most elapids and viperids have a calyculate (reticulate) organ covered with a complex ornamentation of retiform ridges (Text-fig. 5B). In other forms no flounces or calyces are present and the hemipenis is covered with small papillae (Text-fig. 5C). Other hemipenes have an ornamentation of spines (Text-fig. 5D). A relatively few forms have only a single kind of ornamentation (undifferentiated) but more frequently the hemipenis is covered with flounces, calyces, papillae and spines in various regions (differentiated) and in various combinations (Text-figs. 4E, 5B, 6B).

Neither the flounces nor the calyces are simple structures but frequently show rather marked differences in their finer structure (micro-ornamentation). In some instances the ridges are *smooth* (Pl. III, Fig. 5), *scalloped* (Pl. III, Fig. 6, *papillate* (Pl. III, Fig. 7) or *spinulate* (Pl. III, Fig. 8).

Although Cope (1895) described an additional kind of ornamentation, longitudinal folds or plicae, we are convinced that his so-called plicae are longitudinal folds of membranous hemipenial tissue that disappear when the organ is everted (*vide* Dowling, 1959b, p. 2).

In addition to the ornamentation described above, certain species have specialized basal structures. In many forms the spines on the proximal portion of the hemipenis are greatly enlarged to form *basal hooks* (Text-fig. 5D). Bogert (1940, p. 33, fig. 3) has described a large fleshy *basal lobe* in the African natricine colubrid *Neusterophis*. Although he interpreted this condition as representing an example of an asymmetrical double organ, his illustration and the relations of the retractor muscles suggest that this is, instead, a true basal structure. Examination of the hemipenis shows the *m. retractor penis magnus* to be single, while the muscle inserting on the basal lobe is the *m. retractor penis parvus*. If this lobe were merely a reduced segment of a divided hemipenis, the retractor



TEXT-FIG. 6. Apical structure: **A.** Nude (*Natrix sipedon*, HGD 515). **B.** Capitate (*Leptodeira septentrionalis*, HGD 65). **C.** Disked (*Erythrolamprus aesculapii*, HGD 101). **D.** Awned (*Tropidoclonion lineatum*, HGD 198).

should be a divided portion of the *m. retractor penis magnus*. Some snakes of the genus *Atractus* have what appears to be a third type of basal ornamentation, a *basal naked pocket*. However, no fully everted hemipenes of these snakes are available, and the true appearance of this structure is not known.

Apical Differentiation.—The distal end of the hemipenis in most serpents does not differ markedly from adjacent areas in terms of ornamentation. However, in some forms, including species with otherwise undifferentiated organs, there is a sudden change in ornamentation near the apex. Among certain species the tip of the hemipenis is without ornamentation or is *nude*, with a clearly marked line of division between the apex and more basal areas (Text-fig. 6A). A number of forms have the apical region sharply separated from the more basal portion by a deep groove so that the apex is free and the organ is *capitate* (Text-fig. 6B). Others have a flat terminal *disk* on the apex, with the disked area set off from adjoining parts of the hemipenis by raised lips (Text-fig. 6C). Some snakes are characterized by having one or two elongate *terminal awns*, which may project from the apex for a considerable distance (Text-fig. 6D). All of these kinds of apical differentiation are represented within the family Colubridae. Our knowledge of the hemipenes of other serpents does not permit any statement as to the possible occurrence of these structures in non-colubrid snakes.

Summary.—An adequate description of the hemipenes of snakes may be based upon either *in situ* or everted organs. The latter are much to be preferred. It is further suggested that line drawings of the organs are superior to photographs as a method of illustration for systematic purposes. Finally, if only one view of the everted hemipenis is used, illustration of the medial surface, to show the sulcus, is essential. A description of the hemipenis will include data on the following:

Length: longitudinal extent of organ, given in terms of caudal level; possibly also the caudal level at which *m. retractor penis magnus* divides and the caudal vertebrae from which *m. retractor penis magnus* and *m. retractor penis parvus* have their origins.

Shape: whether the organ is simple, bilobed, or divided; whether it is subcylindrical, attenuate, bulbous, clavate or cirrate.

Sulcus Spermaticus: whether simple or bifurcate, location of apical termination; point at which sulcus divides as indicated by caudal level.

Ornamentation: whether the organ is naked or ornamented; whether differentiated or undifferentiated; if ornamented whether with flounces, calyces, papillae or spines; if with flounces or calyces whether the micro-ornamentation is smooth, scalloped, papillate or spinulate; whether there are basal hooks, a basal naked pocket or a basal lobe; pattern and distribution of ornamented areas.

Apical Differentiation: whether the distal end is nude or capitate; whether apex is provided with a terminal disk or terminal awns.

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EXPLANATION OF THE PLATES

Plate I

Cross sections of hemipenes in retracted and everted conditions. Semidiagramatic illustrations indicating the principal features of the hemipenes, penial muscles and associated structures.

Fig. 1. Cross section through tail region of *Lampropeltis getulus* at level of fourth caudal vertebra, showing hemipenes in retracted position.

Fig. 2. Cross section through everted hemipenis of *Natrix erythrogaster*.

Plate II

Longitudinal sections of tail and hemipenes in retracted and everted conditions. Semidiagramatic illustrations of the tail region of *Lampropeltis getulus*, indicating principal structural features and the four penial muscles.

Fig. 3. Left lateral view of parasagittal section through retracted hemipenis and tail (section to left of midline).

Fig. 4. Left lateral view of parasagittal section through everted hemipenis and tail (section to left of midline).

Plate III

Detailed drawings of sulcate surface of hemipenes, showing types of micro-ornamentation.

Fig. 5. *Loxocemus bicolor* (HGD 181), showing smooth calyces.

Fig. 6. *Epicrates angulifer* (HGD 180), showing scalloped flounces.

Fig. 7. *Heterodon platyrhinos* (HGD 512), showing papillate calyces.

Fig. 8. *Spalerosophis diadema* (HGD 16), showing spinulate calyces.